Vol. 257: 1–11, 2003 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published August 7

High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure

Emilio Marañón[1,*], Michael J. Behrenfeld[2], Natalia González[3], Beatriz Mouriño[1], Mikhail V. Zubkov[4]

[1]Departamento de Ecología y Biología Animal, Facultad de Ciencias, Universidad de Vigo, 36200 Vigo, Spain
[2]National Aeronautics and Space Administration, Goddard Space Flight Center, Code 971, Building 33, Greenbelt, Maryland 20771, USA
[3]Departamento de Matemáticas, Física Aplicada y Ciencias de la Naturaleza, Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain
[4]George Deacon Division for Ocean Processes, Southampton Oceanography Centre, University of Southampton, Southampton SO14 3ZH, United Kingdom

ABSTRACT: The oligotrophic waters of the Subtropical Gyres cover >60% of the total ocean surface and contribute >30% of the global marine carbon fixation. Despite apparently uniform growth conditions over broad areas, primary production in these regions exhibits a remarkable degree of variability. In this study of 34 stations in the North and South Atlantic Subtropical Gyres, we found a 20-fold variation (from 18 to 362 mg C m^{-2} d^{-1}) in water-column-integrated primary production rate ($\int$PP), while chlorophyll biomass only varied by a factor of 3. The changes in productivity were not associated with variations in incident surface irradiance, chlorophyll concentration, phytoplankton C biomass or phytoplankton size structure. The rate of nutrient supply to the euphotic layer, as estimated from variations in the depth of nitracline, appeared as the most relevant environmental factor in explaining the observed variability in $\int$PP. We found significant changes in the composition of the picophytoplankton community across the range of measured productivities. The relative biomass contribution of *Synechococcus* spp. and the picoeukaryotes tended to increase with increasing $\int$PP, whereas the opposite was true for *Prochlorococcus* spp. Across the wide range of measured primary productivity rates, the persistent dominance of picophytoplankton indicates that the microbial loop and the microbial food web continued to be the most important trophic pathways. Our observations of the oligotrophic ocean reflect a dynamic ecosystem where the microbial community responds to environmental forcing with significant changes in biological rates rather than trophic organization.

KEY WORDS: Primary production · Chlorophyll · Picoplankton · Size structure · Subtropical Gyres · Atlantic Ocean

INTRODUCTION

In the Subtropical Gyres of the open ocean, the strong vertical stratification of the water column limits the supply of nutrients from below the thermocline to the euphotic layer. As a result, carbon fixation by primary producers in these oligotrophic regions is low (typically below 0.3 to 0.4 g C m^{-2} d^{-1}: see Longhurst et al. 1995). Despite their low areal productivities, these regions, which cover >60% of the total ocean surface area, may account for >30% of the total marine primary production (Longhurst et al. 1995). Time-series studies have shown that photosynthetic C fixation in the Subtropical Gyres displays a significant degree of variability, both at seasonal and interannual time scales (see reviews in Karl et al. 2001, Steinberg et al.

*Email: em@uvigo.es

2001). Given the large impact of the Subtropical Gyres on global biogeochemical budgets, it seems necessary to quantify how variable productivity is within these regions (with both spatial heterogeneity and temporal considered together), identify the causative mechanisms of this variability, and evaluate its implications for large-scale production estimates.

The Atlantic Meridional Transect (AMT) programme represents an effort to study the ecology and biogeochemistry of the upper ocean on very large spatial scales (Aiken & Bale 2000). Previous studies within the AMT programme have reported the latitudinal patterns in picophytoplankton composition (Zubkov et al. 1998, 2000) as well as phytoplankton photophysiology (Marañón & Holligan 1999), production (Marañón et al. 2000) and size structure (Marañón et al. 2001). A comparison of successive AMT cruises suggested that changes in primary production in oligotrophic waters are not associated with significant differences in phytoplankton chlorophyll concentration (Marañón et al. 2000). None of these studies, however, specifically addressed the variability of phytoplankton within the Subtropical Gyres.

From an ecological perspective, variability of primary production in the face of nearly constant phytoplankton biomass poses a number of relevant questions. It has long been assumed that changes in primary production are mostly mediated by an enhancement in the relative contribution of larger cells to total biomass and production. However, the temporal variability in primary production at particular ultra-oligotrophic sites of the Atlantic Ocean do not seem to be associated with major changes in the size structure of the phytoplankton assemblages (Marañón et al. 2001). It is nevertheless possible that variations in primary productivity are related to subtle compositional changes within the picophytoplankton (e.g. Liu et al. 1999) that do not necessarily imply changes in total microbial biomass or size structure. For instance, the relative contribution of *Synechococcus* spp., *Prochlorococcus* spp. and picoeukaryotes to total picophytoplankton abundance has been shown to change markedly during the year in response to hydrodynamical forcing (e.g. Campbell et al. 1997, Gin et al. 1999). However, a specific analysis of the relationship between primary production and picophytoplankton biomass and composition in the Subtropical Gyres of the Atlantic Ocean has not yet been conducted.

The present contribution addresses the variability of phytoplankton biomass and size structure, picophytoplankton composition and primary production in the North and South Atlantic Subtropical Gyres. Specifically, we describe the ecological characteristics of microbial plankton in the Eastern North Atlantic Subtropical Gyre and the South Atlantic Tropical Gyre biogeographic provinces as defined by Longhurst (1998). Our aims were to (1) quantify the combined spatial and temporal variability of C fixation rates, (2) assess the relative importance of different environmental factors in explaining this variability, and (3) investigate the relationship between primary production and community structure in the oligotrophic Atlantic Ocean.

MATERIALS AND METHODS

Sampling was conducted on board the RRS 'James Clark Ross' during May and October 1996, and May and October 1997 as part of the Atlantic Meridional Transect (AMT) programme. At each station, vertical profiles of temperature and salinity were obtained with a Neil Brown Mark IIIB CTD. The vertical attenuation of photosynthetically active radiation (PAR) was calculated with a SeaWiFS Optical Profiling System equipped with a set of 7-channel light sensors. Incident PAR (E_0) was continuously measured by a delta-T Instruments PAR sensor connected to the ship's ocean logger system.

Water samples from 7 to 10 discrete depths were collected at 10:00 to 11:00 h local time using metal-free, lever-action Teflon Go-Flo bottles, which did not have any internal rubber pieces and were provided with silicone O-rings and seals. The bottles had been modified for trace-metal sampling and were mounted on an epoxy paint-coated rosette frame (Bowie et al. 2002). Typically, we collected 3 to 4 samples from the upper mixed layer, 2 to 3 samples from the deep chlorophyll maximum (DCM) and 1 to 2 samples from below the DCM. Micromolar concentrations of nitrate and phosphate were determined on fresh samples using a Technicon AAII autoanalyser and standard techniques. The detection level was 0.05 µM for nitrate and 0.01 µM for phosphate. For each station, the depth of the nitracline was taken to be the first depth where nitrate was detected (>0.05 µM). Size-fractionated chlorophyll *a* concentration was determined fluorometrically after sequential filtration of 250 ml samples through 20, 2 and 0.2 µm polycarbonate filters. Pigment extraction was carried out by keeping the filters in 90% acetone at −20°C overnight. Samples were then analysed using a 10 AU Turner Designs fluorometer, following the non-acidification method. From the surface and the depth of the deep chlorophyll maximum, samples were collected for the microscopic identification and counting of nano- and microphytoplankton following the procedures described in Marañón et al. (2000).